Insect. Soc. 55 (2008) 301 – 312 0020-1812/08/030301-12 DOI 10.1007/s00040-008-1006-5 © Birkhäuser Verlag, Basel, 2008

Research article

Influence of mound construction by red and hybrid imported fire ants on soil chemical properties and turfgrass in a sod production agroecosystem

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Received 10 September 2007; revised 23 April 2008; accepted 1 May 2008. Published Online First 13 June 2008

Abstract. Mound construction by imported fire ants (Solenopsis spp.) actively modify the biogeochemical and physical properties of soil; however, their influence on nutrient levels in surrounding vegetation is poorly understood. Aside from the reported persistence of elevated available P and K levels in clay-rich soils one year after mound abandonment, the relative stability of nutrient concentrations from one season to the next is largely unknown. Nutrient concentrations were concurrently analysed from ant mounds and undisturbed soils as well as plant samples collected from warm-season turfgrass in a commercial sod production agroecosystem. Initial collection of soil and turfgrass samples coincided with peak annual biomass (September 2006); the second soil sample collection occurred over twelve weeks later during turfgrass dormancy and ant brood minimum (December 2006). Total C, C/N ratios, organic matter (OM), and Zn²⁺ concentrations as well as pH of ant mound soils were significantly higher than control plot soils; these trends persisted across seasons. Turfgrass harvested from ant mound perimeters in September exhibited elevated N, P, Ca²⁺, S, Cu²⁺, Fe²⁺, and Na⁺ concentrations. Evaluation of the relative stability of soil parameters across seasons revealed a significant drop in ant nest pH from September to December 2006. Total N of mound soils was distinctively greater than control soil counterparts during September only. Soil P, K⁺, Ca²⁺, Mg²⁺ and S (all macronutrients), as well as Na⁺ concentrations from ant mound soils were substantially elevated during the late Autumn to Winter transition compared to control soil locations, whereas Fe²⁺ and Mn²⁺ levels (both micronutrients) were significantly lower in ant mound soils versus control soil environments. Continuous pedoturbation by imported fire ants as well as seasonal shifts in

mound soil chemistry resulting from changes in assimilation/dissimilation among mound biota may influence the site-specific effectiveness of microfaunal pathogens (e.g., *Thelohania solenopsae*) or parasites (e.g., *Orasema* spp.) identified as classical biological control agents of non-native *Solenopsis* spp. Therefore, further study of the intrinsic complexities of soil ecosystem dynamics of imported fire ant mounds across several seasons is warranted.

Keywords: Mound construction, biogeochemistry, Solenopsis invicta, Solenopsis invicta x S. richteri, turfgrass.

Introduction

Imported fire ants (Solenopsis spp.) modify the ecological properties and dimensionality of invaded environments at multiple scales. Organisms capable of making major alterations to their environment that, in turn, have a profound, cascading influence on habitat structure and function have been referred to as "ecosystem engineers" (Jones et al., 1994; Lavelle, 1997; Alper, 1998). Moundbuilding activities of non-native Solenopsis spp. are known to alter the physical as well as biogeochemical properties of soils. Previously reported changes in the condition of the soil matrix in response to imported fire ant mound pedoturbation (i.e., disturbances or mixing of the soil profile) have included: (1) increased aeration and infiltration (Hays, 1959; Green et al., 1999); (2) altered soil pH (Herzog et al., 1976; Lafleur et al., 2005); (3) increased levels of available P and K⁺ (Herzog et al., 1976; Blust et al., 1982; Green et al., 1998, 1999); (4)

lower surface soil bulk density (Lockaby and Adams, 1985; Lafleur et al., 2005); (5) reductions in organic matter (OM) (Blust et al., 1982; Green et al., 1998, 1999; Seaman and Marino, 2003); (6) lowering of texture grade (Blust et al., 1982; Green et al., 1998, 1999); and (7) greater fungal abundance coupled with lower species richness and diversity (Zettler et al., 2002).

Mound construction by imported fire ant workers results in a complex, dense network of narrow tunnels and nodules constructed of soil pellets mined from deeper horizons; subterranean shafts and nodules excavated through the stoloniferous/rhizomatous mat (at ground level) penetrate downward through the grass root system (5–15 cm depth) linking deeper subterranean true chambers to the above ground portion of the fire ant nest (Markin et al., 1973; Cassill et al., 2002; Tschinkel, 2003). Ant mounds are known to serve as incubators for all brood stages (Cassill et al., 2002).

Previous studies have focused on imported fire ant colonies situated in pasturelands, hay meadows, and forest soils; of these, only one investigation conducted to date reported on the indirect effects of *Solenopsis invicta* Buren mound-building activities on pasture plant composition (Herzog et al., 1976). In Herzog's et al. (1976) work, chemical analyses of grass samples collected from ant mound soils indicated substantially higher concentrations of protein, carotene, and phosphorus. However, these vegetation samples were not directly associated with the original set of pastureland *S. invicta* mounds analysed for soil nutrients, soil pH, and OM.

Imported fire ant nest construction activities are known to alter additional chemical and physical properties of soils; variability of extractable nutrients has been attributed to differences in soil texture (Herzog et al., 1976; Blust et al., 1982). Herzog et al. (1976) examined Ca²⁺ and Mg²⁺ concentrations from S. invicta mounds on Commerce and Sharkey series soils in southern Louisiana. Elevated levels of Ca²⁺ and Mg²⁺ were not detected for ant mound versus control soils at a particular location, although significantly higher levels of these two macronutrients were reported for unimproved cattle pasture on clay-rich Sharkey soils (very-fine, smectitic, thermic Chromic Epiaquerts – USDA-NRCS, Official soil series descriptions, http://www2.ftw.nrcs.usda.gov/cgi-bin/osd/osdname.cgi) compared to improved pasture sited on friable Commerce silt loam soils (finesilty, mixed, superactive, nonacid, thermic Fluvaquentic Endoaquepts). Similarly, OM contents were substantially higher on Sharkey clay compared to Commerce silt loam, however, no statistically significant differences were observed between ant mound and control soils at either pastureland site. Wangberg et al. (1980) found no differences in pH or OM (%) when comparing S. invicta mound versus non-mound soil samples distributed across 19 counties in East Texas. In addition, Wangberg and associates conducted an examination of soil textural conditions that may favour red imported fire ants; however, results were inconclusive. Blust et al. (1982)

reported increased available P and K⁺ levels, increased proportion of clay-sized particles, and reduced OM content from *S. invicta* mounds versus nearby undisturbed surface soils in Louisiana pasture dominated by Sharkey clay. They also noted that P and K⁺ concentrations from purposefully killed ant mounds remained at or near recorded levels even after one year.

Lockaby and Adams (1985) investigated the effects of S. invicta on forest soils of north central Louisiana, and provided stratified details on the physicochemical modifications found within ant mounds. Their study sites occurred on Kirvin (fine, mixed, semiactive, thermic Typic Hapludults) and Boswell (fine, mixed, active, thermic Vertic Paleudalfs) series soils; all three sites had been clearcut, planted with loblolly pine (*Pinus taeda* L.) and were in the third growing season. These authors noted that the top 5 cm of S. invicta mounds were lower in bulk density and significantly higher in OM, P, K⁺, Ca²⁺, and Mg²⁺ concentrations than nearby surface soils. However, ant mound soil samples extracted from the 15–20 cm depth exhibited markedly elevated OM and K⁺ levels only. Comparison of ant mound versus undisturbed soil pH revealed no significant differences, and was postulated to be related to E (eluviated) horizons with sandy loam texture on two of the three study sites (Lockaby and Adams, 1985).

Davis-Carter and Sheppard (1993) evaluated the redistribution of select heavy metals and nutrients in a bahia grass (Paspalum notatum Flüggé) pasture on Bonifay series soils (loamy, siliceous, subactive, thermic Grossarenic Plinthic Paleudults) in the coastal plain of Georgia. Their results indicated significantly elevated K⁺ and Mg²⁺ concentrations in ant mounds versus control areas; however, available P and Zn²⁺ were substantially lower in mounds than in control areas. Increases in K⁺ and Mg²⁺ were attributed to the accumulation of clay (i.e., kaolinite) in the upper mounds. In addition, Mn²⁺ concentration was significantly higher in ant mounds (at the 0-15 cm depth) than in control areas. There were no significant differences in soil pH, total Cd²⁺, total Cr²⁺, total Pb2+ and total Zn2+ concentrations between ant mounds and the surrounding soil. In closing, Davis-Carter and Sheppard (1993) commented that S. invicta may actively avoid Zn²⁺ during mound construction although a threshold value of mg Zn kg⁻¹ was not specified in their

Green et al. (1998, 1999) examined the impacts of imported fire ants (including red, black, and putative hybrids) on soil texture and fertility across nine soil series (representing five soil orders) in Mississippi; however, replicated studies were performed only from the contrasting soils of a pine plantation on Malbis fine sandy loam (fine-loamy, siliceous, subactive thermic Plinthic Paleudults) and unimproved pasture mapped as Vaiden clay (very-fine, smectitic, thermic Aquic Dystruderts). Notable differences in the ant mound environment compared to surrounding surface soils (typically upper 5 cm) included higher clay content, lower OM, and higher

concentrations of available P and K^+ in imported fire ant nests. Variability in Ca^{2+} and Mg^{2+} concentrations were attributed to trends observed in soil mixing patterns among study sites as well as the subsoil contents of these two macronutrients in undisturbed soil profiles (Green et al., 1998, 1999).

Seaman and Marino (2003) compared a comprehensive suite of nutrients as well as soil pH and OM contents from *S. invicta* mound soils (top 15 cm) and undisturbed old-field soils from the coastal plain of South Carolina. Nitrate concentration (NO₃-N) was significantly higher for ant nest soils compared with control soils; whereas undisturbed soils exhibited markedly higher OM, extractable P, Mg²⁺, Cu²⁺, and Zn²⁺ levels. Concentrations of K⁺, Ca²⁺, B, Mn²⁺ and soil pH were not significantly different between ant mound and undisturbed old-field soil samples (Seaman and Marino, 2003).

Lafleur et al. (2005) conducted an interesting set of experiments in greenhouse and field settings. Under controlled greenhouse conditions, *S. invicta* activities decreased soil pH, and increased available P and K⁺ concentrations. Ant nest soils from long-leaf pine (*Pinus palustris* Mill.) forests were significantly higher in extractable P, K⁺, Ca²⁺, Mg²⁺, and Na⁺ compared to adjacent undisturbed soils, however, ant nest soils obtained from young (< 5 y) long-leaf pine plantations had markedly higher extractable P levels only. The dominant mineral N form for both habitats was NH₄⁺ with concentrations higher in *S. invicta* mounds. No effect on soil pH was reported for both pine forests and pine plantations (Lafleur et al., 2005).

In this investigation, we extend and expand upon the works of Herzog et al. (1976), Blust et al. (1982), Davis-Carter and Sheppard (1993), and Green et al. (1998, 1999) all of whom focused, for the most part, on imported fire ant impacts in grass-dominated agroecosystems. Emphasis has also been placed on sampling ant mound and control plots during two key phases of the annual nesting cycle of imported fire ants as well as testing for differences in the temporal stability of these changes in soil chemistry across seasons from late Summer to the late Autumn-Winter transition. Peak biomass of S. invicta from individual ant mounds has been reported for the months of May and October in the northern hemisphere; October has been identified as the annual maximum (Lofgren et al., 1975). Another investigator has noted the end of August or mid-September (observations were made in New Orleans, LA and Poplarville, MS, USA, respectively) as the interval of peak annual biomass for S. invicta (Rojas 2007, pers. comm.). The objectives of this study were twofold: (1) compare select soil parameters in ant mound and undisturbed soils along with plant nutrients in ant-affected versus undisturbed turfgrass from a commercial sod production setting during the late Summer (coinciding with peak imported fire ant biomass); and (2) re-examine soil chemical properties when turfgrass was dormant (and brood biomass was at or near annual minimum) during the late Autumn to Winter season

transition in order to assess the temporal stability of these soil parameters between control and ant mound soil environments.

Those invertebrates that reside in the soil may markedly influence soil quality and crop nutrient management efforts at field-, landscape-, and possibly regional scales (Lal, 1988). Jones et al. (1994) classified ants as ubiquitous allogenic engineers that not only impact the local structure and chemical composition of soil, but also alter 'above nest' vegetation and produce microsite enrichment. Lobry de Bruyn (1999) commented that ants may have a resilient role in maintaining soil quality in agricultural landscapes (by digging, pelleting and mixing horizons in the soil profile) due to their ability to survive and thrive in these settings despite disturbance regimes. Detailing imported fire ant assimilation/dissimilation effects on the soil matrix at key stages in their annual life cycle may reveal avenues for the development of better integrated biological-geochemical control techniques for curbing their spread into high maintenance and intensive industries such as turfgrass. The turfgrass industry in the United States, for example, generated total output (revenue) impacts of \$62.2 billion, expressed in 2005 US dollars (Haydu et al., 2006). In addition, results from this study may help improve remote-sensing detection tools useful in identifying and monitoring imported fire ant infestations in high-value turfgrass systems.

Materials and methods

Site description

This investigation was conducted on a commercial turf farm located in the Southern Mississippi Valley Silty Uplands (MLRA 134), USA (33°30′N, 89°52′W). Red imported fire ants (*S. invicta*) as well as hybrids (*S. invicta* Buren x *S. richteri* Forel) are known to occur in the countywide (165,241 ha) area (Streett et al., 2006). The terrain was undulating (0–8% slopes) with local topography varying from 73–82 m in elevation. Turfgrass (*Cynodon dactylon* (L.) Pers x *C. transvaalensis* Burtt-Davy, cv. Tifway 419, an F₁ hybrid bermuda grass) was maintained at a mowing height of 3–4 cm, and mowed 2–3 times per week throughout the Summer and Autumn.

Three soil series have been mapped to the field site, and include Ariel (coarse-silty, mixed, active, thermic Fluventic Dystrudepts), Calloway (fine-silty, mixed, active, thermic Aquic Fraglossudalfs) and Loring (finesilty, mixed, active, thermic Oxyaquic Fragiudalfs) silt loam soils. Reported surface soil pH is \leq 5.5, and effective cation exchange capacity (ECEC) is low, ranging from 2.8-5.9 cmol_c kg⁻¹ (USDA, Natural Resources Conservation Service URL http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx). Agricultural practices in this commercial sod production system served to homogenize the soil chemistry (to a depth of at least 5 cm) of the three silt loam soils mapped to this field. The last application of fertilizer (168 kg NH₄NO₃ ha⁻¹) was delivered in early May 2006. Irrigation (2.5 cm increments) was typically delivered every 7-10 d, depending on weekly water balance in this predominantly rainfed agroecosystem. Total rainfall (1 September-18 December 2006) was 584 mm. Compared to the 30-y average (1971-2000), precipitation was above normal for the months of September (+154.7 mm) and October (+137.9 mm), but below normal for November (-47.0 mm) and December (-15.7 mm). No supplementary irrigation events were recorded during the study interval.

Ant identification and social form determination

Worker ants were identified based on cuticular hydrocarbon and venom alkaloid composition as analysed by gas chromatography and mass spectrometry (GC-MS). Additional details on GC-MS system setup and sample processing protocols have been outlined by Chen (2007). Species identification was performed on sixteen colonies, and five cuticular hydrocarbon peaks as well as four venom alkaloid peaks were used in the taxonomic determinations (Vander Meer, 1986; Ross et al., 1987; Vander Meer and Lofgren, 1988).

Solenopsis invicta social form was determined by purifying DNA from a group of 20–30 ants per nest stored in 70% isopropanol. The DNA extraction method used as well as the PCR cycling parameters were outlined by Chen and Allen (2006). Both positive (polygyne) and negative (no DNA) controls were processed along with the samples.

Analysis of soil and turfgrass

Paired soil samples from active imported fire ant mounds (n = 10) and nearby control soil locations (n = 10) were obtained on 20 September 2006 from the turfgrass agroecosystem. Control locations were typically 2-3 m from an active mound and bearing no evidence of soil disturbance by the ants. Collection sites were distributed evenly across the field with 3 to 4 paired samples obtained for each soil series. Mound soils were collected in entirety to a depth of 5 cm beneath the soil surface from nests in classes 9 or 10 of the Harlan et al. (1981) rating system (i.e., approximately 30-60,000 workers and brood present). Each sample was carefully placed on a non-reactive surface (so that most ants could escape, however, control soils were handled in an identical manner), then placed in a plastic bag, sealed and stored in a cooler (4 °C) for transport to the laboratory. Remaining ants and brood were removed by sieving and use of sterile forceps within 18-20 h of soil collection. Soils were subsequently air-dried, ground, and passed through a 2-mm sieve. Standard soil analyses included: (1) soil pH (1:1 with deionized water); (2) OM%; (3) total C% and total N%; (4) Mehlich 3 extractions for $P, K^+, Ca^{2+}, Mg^{2+}, Cu^{2+}, Zn^{2+}, Na^+, and S$; and (5) diethylene triamine pentaacetic acid (DTPA) extractions for Cu²⁺, Zn²⁺, Fe²⁺, and Mn²⁺. Organic matter (%) was determined using the Walkley-Black procedure (Walkley and Black, 1934; Walkley, 1947). Total C% and total N% were evaluated by dry combustion using a LECO TruSpec CN analyzer (LECO Corporation, St. Joseph, MI, USA). Concentrations of soil macronutrients and micronutrients were determined using a Spectro Ciros CCD ICP optical emission spectrometer (Spectro Analytical Instruments, Kleve, Germany). Prior to sampling, mound meristics were acquired; GPS coordinates of all mound locations were obtained post-sampling.

Turfgrass plant samples were hand-cut from ant mound perimeters $(n\!=\!10)$ as well as from adjacent undisturbed turf $(n\!=\!10,$ approximately 2 m from mound edge), placed in paper bags, then sealed within individual plastic bags, and stored in a separate cooler $(4\,^\circ C)$ for transport. Turfgrass samples were allowed to air-dry (at room temperature) upon immediate return to the laboratory for 36–48 h. Plant tissue analyses included ppm $(mg~kg^{-1})$ determinations for B, $Cu^{2+},$ $Fe^{2+},$ $Mn^{2+},$ Mo, $Na^+,$ and Zn^{2+} as well as percentages of N, P, $K^+,$ $Ca^{2+},$ $Mg^{2+},$ and S. Specific procedures used by the Louisiana State University AgCenter Soil Testing and Plant Analysis Laboratory are available online (URL http://www.lsuagcenter.com/en/our_offices/departments/ Agronomy_Environmental_Management/soil_testing_lab/procedures/Procedures+Used+at+the+Laboratory.htm).

Over twelve weeks later (18 December 2006), additional paired soil samples from active imported fire ant mounds (n=14) and proximate control soil locations (n=14) were collected from this agroecosystem. These fourteen paired sites (ant mound versus control) were located within 1-5 m of the original ten mound-control paired locations, and distributed as evenly as possible across the three soil series mapped to the field (with 4 or 5 mounds collected per soil series). Colonies were assigned ratings of 4-5 (Harlan et al., 1981) based on visual estimation of ant numbers. Soil samples were processed in the same manner as described for the September

collection date; in addition, the same suite of standard soil analyses were performed.

Statistical analysis

Datasets were initially separated by soil series for statistical analysis, however, significant differences were lacking, and therefore the three groups were merged. These data were analysed as a randomized complete block design with a pair-wise grouping of an imported fire ant mound location and adjacent undisturbed (control) area as a blocking factor, and the two soil environments (i.e., ant mound versus control) as treatments. Data for each block were obtained for soils on two collection dates (20 September and 18 December 2006) and plant samples from actively-growing turfgrass were harvested on one date (20 September 2006).

All data were log transformed to help meet the assumptions of equal variances and normality between the two soil environments (ant mound versus control). Soils and turfgrass datasets were analysed separately using Proc Mixed (Littell et al., 1996) because the equal variance requirement between these two groups was not met in several cases, even on the log scale. F-tests were used to compare soils and turfgrass sample data means by soil environment (or treatment) as well as detect seasonal interactions based on ANOVAs of log-transformed values. Reported means were back-transformed from the log scale (i.e., geometric means); least significant differences (LSD) on the log scale were back-transformed to represent a ratio of the geometric means and are referred to as least significant ratio (LSR). Pearson product-moment correlation coefficients were calculated based on the log-transformed dataset. Differences in means as well as correlations (r) were reported as significant at $\alpha\!=\!0.05$.

Results

Red and hybrid imported fire ants were recorded at this locality as well as an admixture of monogyne and polygyne mounds. In addition, subsamples of ants from individual ant mounds indicated the co-occurrence of monogyne and polygyne social forms. Continuous sod harvesting efforts (May-December) made it challenging to assess actual nest density due to repeated fragmentation of mounds in some areas of the field. At the close of December 2006, close to 90% of the turfgrass had been harvested from this bermuda grass tract.

Total C, C/N ratios, OM, and Zn²⁺ concentrations as well as pH levels of mound soils were significantly higher than control plot soils; these trends persisted over a period of 12 weeks (Table 1). Total N of ant mound soils was distinctively greater than control plot counterparts during the late Summer to Autumn transition only. Soil P, K⁺, Ca²⁺, Mg²⁺, S (all macronutrients), and Na⁺ concentrations from ant mounds were substantially elevated during the Autumn to Winter transition compared to control plots, whereas Fe²⁺ and Mn²⁺ levels (both micronutrients) were significantly lower in ant mound soils versus control soil samples.

The relative stability of these soil parameters across seasons was also evaluated. Analysis of seasonal interactions highlighted a significant drop in ant mound soil pH from September to December 2006 (Table 1). Copper concentrations (Cu-DTPA extraction method only) increased sharply from late Summer to late Autumn for

Table 1. Mean chemical properties of soil from ant mounds and control plots.

Soil Property	20 Sep 2006			18 Dec 2006	5		Seasonal Interaction	on (df 1,22)
	Mound (n=10) §	Control (n=10) §	LSR‡	Mound (n = 14) §	Control (n=14) §	LSR‡	Mound F value (P)	Control F value (P)
pН	6.04	5.49	1.06**	5.64	5.37	1.04*	6.91 (0.0153)	0.71 (0.4074)
C/N ratio	6.63	5.76	1.15*	6.10	5.32	1.07***	2.43 (0.1331)	2.11 (0.1609)
OM (%)	1.45	0.95	1.16***	1.51	1.08	1.18***	0.18 (0.6724)	1.73 (0.2014)
Total C (%)	0.80	0.52	1.19***	0.64	0.52	1.15**	3.86 (0.0622)	0.02 (0.9029)
Total N (%)	0.13	0.10	1.14***	0.11	0.11	1.08	2.96 (0.0997)	1.19 (0.2868)
P (mg/kg)	50.51	39.18	1.53	41.65	25.80	1.19***	0.86 (0.3644)	4.02 (0.0573)
K ⁺ (mg/kg)	214.67	194.16	1.15	199.98	148.54	1.10***	0.69 (0.4163)	9.80 (0.0049)
Ca^{2+} (mg/kg)	953.82	815.41	1.42	1063.56	630.59	1.15***	0.71 (0.4087)	3.95 (0.0594)
Mg^{2+} (mg/kg)	116.44	94.42	1.46	156.73	90.19	1.18***	2.31 (0.1430)	0.06 (0.8165)
S (mg/kg)	11.05	13.13	1.36	26.66	16.94	1.19***	57.25 (< 0.0001)	4.79 (0.0395)
Cu^{2+} (mg/kg)	1.06	0.98	1.23	1.18	1.09	1.16	0.73 (0.4030)	0.75 (0.3961)
Cu^{2+} $(mg/kg)^{\dagger}$	0.55	0.50	1.25	0.93	1.03	1.15	14.77 (0.0009)	27.26 (< 0.0001)
Zn^{2+} (mg/kg)	0.97	0.62	1.27**	0.85	0.66	1.29	0.51 (0.4815)	0.09 (0.7625)
Zn^{2+} $(mg/kg)^{\dagger}$	0.49	0.31	1.24***	0.62	0.43	1.24**	2.15 (0.1566)	3.78 (0.0647)
$\mathrm{Fe^{2+}}(\mathrm{mg/kg})^{\dagger}$	54.19	63.47	1.33	45.36	62.39	1.12***	2.35 (0.1393)	0.02 (0.8844)
Mn^{2+} $(mg/kg)^{\dagger}$	56.79	71.08	1.60	22.38	34.06	1.22***	21.02 (0.0001)	13.12 (0.0015)
Na ⁺ (mg/kg)	21.08	16.43	1.62	22.79	17.61	1.20**	0.24 (0.6258)	0.19 (0.6651)

[†] DTPA micronutrient extraction method.

both ant mound and control soil samples. Similarly, S levels in these two soil environments exhibited marked increases from September to December. In contrast, $\mathrm{Mn^{2+}}$ concentrations diminished sharply from both ant mound and control soil samples during this interval. Although not significant at $\alpha = 0.05$ (Table 1), total C (%) of ant mounds declined from late Summer to late Autumn (P = 0.0622). In addition, noteworthy decreases in available P (P = 0.0573) and $\mathrm{Ca^{2+}}$ (P = 0.0594) concentrations were detected in the control soil environments; however, $\mathrm{Zn^{2+}}$ concentration (DTPA extraction only) increased from September to December in control soils (P = 0.0647).

Turfgrass harvested from ant mound perimeters (20 September 2006) exhibited significantly higher N, P, Ca²⁺, S, Cu²⁺, Fe²⁺, and Na⁺ concentrations (Table 2). Elevated N levels as well as C/N ratios were detected in the ant mound soils; however, P, Ca²⁺, S, Cu²⁺ (both Mehlich 3 and DTPA extraction methods), and Fe²⁺ contents between ant mound and control soil samples were not significantly different at this time (Table 1). The effects of myrmecochory were not evident on this sod production farm during the study period (DeFauw, 2006, pers. obs.).

Comparison of Pearson product-moment coefficients for imported fire ant mound soils from the two sampling dates permitted the detection of nutrient level associations as well as contrasts from September (coinciding with

Table 2. Comparison of turfgrass nutrient concentrations (*Cynodon dactylon x C. transvaalensis*, Tifway 419 cultivar) from ant mound perimeters and control plots.

Turf Analysis	20 Sep 2006		
	Mound (n=10) §	Control (n=10) §	LSR [‡]
Total N (%)	2.45	1.80	1.21**
P (mg/kg)	2573.32	2189.34	1.11**
K^{+} (mg/kg)	14484.21	12507.46	1.21
Ca^{2+} (mg/kg)	4328.06	4009.77	1.05**
Mg^{2+} (mg/kg)	1325.41	1243.05	1.20
S (mg/kg)	2384.27	1936.96	1.11**
Cu^{2+} (mg/kg)	9.81	8.31	1.14*
Zn^{2+} (mg/kg)	30.88	27.09	1.24
$\mathrm{Fe^{2+}}$ (mg/kg)	397.20	151.11	1.64**
Mn^{2+} (mg/kg)	195.61	178.32	1.13
B (mg/kg)	6.55	7.14	1.33
Na+ (mg/kg)	831.83	507.88	1.42*

[§] Means were back-transformed from the log scale (i.e., geometric means).

[§] Means were back-transformed from the log scale (i.e., geometric means).

[‡] Least Significant Difference (LSD) on log scale was transformed to Least Significant Ratio (LSR).

^{***} P < 0.001; ** P < 0.01; * P < 0.05.

[‡] Least Significant Difference (LSD) on log scale was transformed to Least Significant Ratio (LSR).

^{***} $P \le 0.001$; ** $P \le 0.01$; * $P \le 0.05$.

peak imported fire ant biomass) to December (brood biomass at or near annual minimum). Calcium (Ca²⁺) concentration was significantly correlated with C/N ratio, OM, C, N, and Na⁺ during the late Summer to Autumn transition only. Similarly, Na⁺ was significantly associated with OM, C, N, Ca²⁺, and Mg²⁺ for the September sampling date; significantly correlated associations for Mg²⁺ included OM, C, N, and Ca²⁺. Over twelve weeks later (December), P was significantly correlated with OM, C, N, Cu-DTPA, Zn-DTPA, and S during the late Autumn to Winter transition only (Table 3). In addition, Cu²⁺ and Fe²⁺ (DTPA extraction method for both elements) were highly correlated with C/N ratio, OM, C, and N. Manganese (Mn²⁺) and S were both negatively correlated with Mg²⁺.

Correlation coefficients for undisturbed (control) soils from the September collection date were notably different in overall patterns of significance from imported fire ant mound soils (Table 4). Calcium (Ca²⁺) was highly associated with macronutrients N, P, K⁺ and S as well as Na⁺. Copper (Cu²⁺) was significantly correlated with OM, total C, total N during September only. In addition, Na⁺ was well-correlated with N, K⁺, Ca²⁺, Mg²⁺, Cu²⁺ (Mehlich 3 extraction only), and S. Sulfur (S) was also positively associated with N, Mg²⁺, and Zn-DTPA. Over twelve weeks later (December), P was highly associated with Cu²⁺ and Zn²⁺ (for both Mehlich 3 and DTPA extraction methods) as well as Fe²⁺, and negatively correlated with Mg²⁺. Calcium (Ca²⁺) and Na⁺ were positively correlated with pH, whereas Fe²⁺ and S were negatively correlated with pH.

Discussion

Soils altered by imported fire ant mound-building activities have been termed "formicarious pedons" (Green et al., 1999) based on structural as well as compositional modifications. However, details on the temporal stability of soil chemical alterations are very poorly understood. Three principal emergent findings from this investigation include: (1) soil modifications as a consequence of ant mound construction exhibited varying levels of stability from one season to the next; (2) control soils differed from ant mound soils in their patterns of nutrient retention or loss across seasons; and (3) contrasts in correlation of nutrients between the two soil environments (ant mound versus control soil) from September to December 2006 suggests that plant status (active versus dormant) also contributed to the complexity of soil system dynamics in ant mound versus control soils.

Differences in observed OM content, nutrient concentrations, and pH between ant mound and control soil environments are in agreement with some of the previously-published findings. For example, in this investigation OM content was greater in imported fire ant mound soils which supports one of the conclusions of Lockaby and Adams (1985), but contradicts summary

information reported by Blust et al. (1982) and Green et al. (1998, 1999). Increased OM content affects soil properties by improving moisture retention, facilitating soil warming, enhancing buffering capacity, and mineralizing to yield additional nutrients including NO₃-N, $H_2PO_4^-$, and SO_4^{2-} (Stevenson, 1982). Soil OM also improves soil structure by promoting aggregate formation (Stevenson, 1982) which may, in turn, help stabilize ant biopores and mound architecture. During August through December, imported fire ants were observed covering mounds with bermuda grass thatch (dried blades typically 1.0-1.5 cm in length); thatch density varied from two to several layers thick and appeared to be used as structural support when upper walls and ceilings of mound tunnels were repaired (DeFauw, 2006, pers. obs.). Blust et al. (1982) and Green et al. (1998, 1999) conducted their investigations on hay meadow and pasture soils where disturbances in the root zone may have been minimal compared to soil profile disturbances caused by clear-cutting trees or harvesting sod. Enhanced incorporation of organic residues in non-native Solenopsis spp. mounds may be a response to increasing severity of topsoil disturbance; further study of this proposed interaction is warranted as OM influences soil aggregate formation and stabilization (e.g., Abiven et al., 2007), macro- and micronutrient availability (e.g., Stevenson, 1982), and soil pH (e.g., Stevenson, 1982).

Significant contrasts in available P and K⁺ levels from ant mound versus control soils were detected in December (with higher P and K⁺ concentrations in imported fire ant mound soils), but not in September 2006. Previous investigators reported elevated P and K⁺ levels in S. invicta ant mounds from their collective Spring to Summer sampling efforts (Herzog et al., 1976; Blust et al., 1982; Green et al., 1998, 1999). Recently, Chen (2005) documented the excretion of phosphoric acid by S. invicta in artificial nests with workers producing 0.08 ± 0.024 µg/ant/d under confined laboratory conditions. Chen (2005) also remarked that phosphoric acid can decrease the pH of mound materials, which may assist in impeding microbial growth in S. *invicta* ant mounds. However, the artificial nesting medium (silica gel) is not comparable to native soils in terms of buffering capacity, though it is highly certain that acidic microsites in the soil matrix perform the function just described. In this study, available P from ant mound soils was significantly correlated with OM, N, S and Cu^{2+} and Zn^{2+} in December 2006 (Table 3). Possible contributing sources for elevated P in these ant mound soils may include: (1) OM decomposition; (2) organic anion replacement of H₂PO₄⁻ on adsorption sites (e.g., malate and malonate – Tisdale et al., 1993); (3) seasonal turn-over in the rhizosphere; and (4) low temperatures constraining ant movements.

In this study, ant mound soil pH was substantially higher than undisturbed soil plots on both collection dates; only Herzog et al. (1976) reported on this direct

Table 3. Pearson product-moment coefficients for imported fire ant mound soils. Correlation coefficients for 20 September 2006 are displayed above the values for 18 December 2006 for comparison.

сошранвоп.	п.															
Hd	C/N	ОМ	C	Z	I I	K	Ca	Mg	Cu	$\mathbf{C}\mathbf{u}^{\dagger}$	Zn	$\mathbf{Z}\mathbf{n}^{\dagger}$	${f Fe}^{\dagger}$	\mathbf{Mn}^{*}	Na	S
									mg/Kg	24						
pH 1.000	0 0.432 0.383	0.515 0.377	0.493 0.319	0.456 0.237	0.623 0.258	0.445 - 0.178	0.425 0.398	0.127 0.418	$0.470 \\ 0.413$	0.449 0.261	0.625 0.422	0.604	-0.569 -0.238	-0.570 -0.408	0.098	0.215 - 0.136
C/N	1.000	0.602	0.857** 0.931***	0.626 0.783***	0.081 0.498	-0.284 0.147	0.665*	0.366 -0.027	0.570 0.829***	0.604	0.675* 0.854***	0.646* 0.888***	-0.146 $0.668**$	0.051	0.440 - 0.010	-0.314 -0.020
OM		1.000	0.830**	0.850**	0.332	0.327	0.748* 0.340	0.683* 0.144	0.349	0.514 0.869***	0.661* 0.913***	0.784** 0.948***	0.073	0.090	$0.757* \\ -0.167$	$-0.205 \\ 0.081$
C			1.000	0.938***	0.237 0.644*	0.081	0.832** 0.374	0.718* 0.026	0.422 0.882***	0.573	0.701* 0.923***	0.784**	-0.090 0.659*	-0.082 0.235	0.662* -0.118	-0.390 0.092
z				1.000	0.304	0.312 0.607*	0.812** 0.420	0.841**	0.258	0.464	0.608	0.753*	-0.036 $0.587*$	-0.161 0.088	0.705* -0.194	-0.381 0.173
Ь					1.000	0.425 0.351	0.215	-0.037 -0.203	0.673*	0.584	0.670* 0.782***	0.515	- 0.093 0.448	-0.598 -0.132	-0.108 -0.132	0.340
X						1.000	0.109 0.142	0.332 0.094	-0.174 0.162	-0.060 0.362	0.086 0.346	0.293	-0.136 0.313	$-0.275 \\ -0.114$	$0.200 \\ -0.257$	0.169 0.181
Ca							1.000	0.768**	0.144 0.367	0.185	0.428 0.423	0.545 0.431	-0.333 -0.302	0.054 -0.484	0.824** 0.387	-0.233 -0.081
Mg								1.000	-0.215 -0.143	-0.032 -0.087	0.145 0.032	0.424 0.129	-0.023 -0.485	0.173 $-0.708**$	0.883*** 0.152	$-0.515 \\ -0.577*$
Cu									1.000	0.925***	0.880*** 0.901***	0.622 0.898***	0.138 0.497	-0.319 0.224	-0.172 -0.061	0.126 0.283
Cu^{\dagger}										1.000	0.915*** 0.921***	0.720* 0.938***	0.292 0.664**	-0.337 0.288	-0.064 -0.037	-0.046 0.183
Zu											1.000	0.908*** 0.965***	$0.006 \\ 0.546*$	-0.293 0.065	0.169 - 0.118	0.149 0.181
$\mathbf{Z}\mathbf{n}^{\dagger}$												1.000	-0.074 $0.551*$	-0.117 0.086	0.444 - 0.103	0.135 0.103
Fe⁺													1.000	0.320	-0.051 -0.259	-0.406 0.083
Mn^{\dagger}														1.000	$0.492 \\ -0.075$	-0.095 0.035
Na															1.000	-0.303 0.085
S																1.000

 † DTPA extraction. *** $P\!\leq\!0.001;$ ** $P\!\leq\!0.01;$ * $P\!\leq\!0.05$

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Table 4. Pearson product-moment coefficients for undisturbed (control) soils. Correlation coefficients for 20 September 2006 are displayed above the values for 18 December 2006 for comparison.

comparison.	on.															
Hd	S	ОМ	C	Z	Ь	K	Ca	Mg	Cu	$\mathbf{C}\mathbf{u}^{\dagger}$	Zn	$\mathbf{Z}\mathbf{n}^{\dagger}$	\mathbf{Fe}^{\dagger}	Mn⁺	Na	S
									mg/Kg	56						
pH 1.000	- 1	0.239 0.146 0.056 0.102	0.124 0.068	0.243	0.669*	0.596	0.534 0.721**	0.319 0.528	0.481 -0.196	0.305 -0.317	0.670* -0.154	0.508 -0.228	-0.746* $-0.573*$	-0.856** -0.513	0.555 0.552*	0.334
C/N	1.000	0.215	0.310	-0.156 $0.748**$	0.078 0.126	$-0.699* \\ -0.138$	-0.465 0.378	-0.363 0.093	-0.044 $0.578*$	0.043 $0.631*$	0.067 0.516	0.069	0.577	0.437 0.111	-0.432 0.138	-0.329 0.172
OM		1.000	0.928***	0.861** 0.869***	0.059 0.153	$0.077 \\ -0.071$	0.611 0.519	0.526 0.163	0.635* 0.471	0.710* 0.498	0.457 0.570*	0.585	0.122 0.420	-0.100 0.120	0.426 0.181	0.484 0.152
C			1.000	0.891***	0.043	$0.059 \\ -0.045$	0.550 0.482	0.495 0.178	0.718* 0.470	0.793** 0.544*	0.514 0.536*	0.506	0.141 0.422	-0.072 0.078	0.521 0.071	0.558 0.169
z				1.000	0.008	0.395	0.792** 0.527	0.687* 0.240	0.768** 0.296	0.805**	0.503	0.660*	-0.130 0.388	-0.285 0.031	0.749* -0.005	0.738*
Ь					1.000	$0.129 \\ -0.456$	0.101 - 0.479	-0.244 $-0.734**$	0.245 $0.601*$	$0.102 \\ 0.548*$	0.597	0.524 $0.615*$	-0.251 $0.578*$	-0.303 -0.098	$0.155 \\ 0.016$	0.196
X						1.000	0.740* 0.272	0.605 0.450	$0.179 \\ -0.580*$	0.077 - 0.439	0.111 - 0.611*	$0.122 \\ -0.566*$	-0.724* -0.338	$-0.677* \\ -0.071$	$0.683* \\ -0.412$	0.343 - 0.057
Ca							1.000	0.827** 0.825***	0.498 - 0.139	0.460 - 0.159	0.326 -0.046	$0.395 \\ -0.132$	-0.568 -0.381	-0.564 -0.329	0.823** 0.445	0.698* 0.471
Mg								1.000	0.398 - 0.451	0.323 - 0.424	$0.253 \\ -0.350$	0.311 - 0.351	-0.604 $-0.588*$	-0.534 -0.313	0.817** 0.147	0.654* - 0.422
Cu									1.000	0.944***	0.840** 0.854***	0.821** 0.876***	-0.214 $0.781***$	-0.521 0.342	0.648*	0.624 0.120
Cu⁴										1.000	0.711* 0.795***	0.759*	0.032	-0.295 0.417	0.508	0.550 0.184
Zn											1.000	0.941*** 0.938***	-0.338 $0.728**$	-0.542 0.228	0.559 0.175	0.590
$\mathbf{Z}\mathbf{n}^{\dagger}$												1.000	-0.191 $0.782***$	-0.340 0.322	0.607 0.034	0.714*
$\mathrm{Fe}^{\scriptscriptstyle +}$													1.000	0.866**	$-0.697* \\ -0.188$	-0.439 0.375
$\mathrm{Mn}^{\scriptscriptstyle +}$														1.000	-0.658* -0.248	-0.318 0.308
Na															1.000	0.857** -0.380
S																1.000
† DTPA extraction	vtraction															

*** $P \le 0.001$; ** $P \le 0.01$; * $P \le 0.05$

effect of *S. invicta* on pasture soils in Louisiana. Soil pH is influenced by types of organic matter and mineralogy of clay fractions as well as their associated exchangeable cations (e.g., Ca²⁺, Mg²⁺, K⁺, Na⁺, Al³⁺, H⁺); a good, general overview of this topic has been provided by Sposito (1989). At this juncture, it is worthwhile to focus on a more soil-oriented framework for the interpretation of some additional apparent inconsistencies among previously-published papers on the influences of imported fire ant mound-building activities on soil chemistry and the current study.

Soil properties that contribute to soil quality have been classified based on their relative permanence and sensitivity of response to management practices in agroecosystems (Islam and Weil, 2000). Some soil properties such as pH, water content, bulk density, mineral N, available K+, labile P, and field soil respiration are considered to be ephemeral; these may change over the course of hours to days in response to routine management and weather conditions. The most stable soil properties are inherent to a particular site's historical landscape features (i.e., topography and parent material), and soil profile development as influenced by climate, biota, subsurface hydrology and time; these properties include texture, solum depth, mineralogy, slope, restrictive horizons, and stoniness. In agroecosystems, the intermediate class of soil-quality indicators is subject to management over the course of several years, such as soil OM content and active C levels, along with soil aggregation and microbial biomass (Islam and Weil, 2000). Bioturbators, especially invasive soil-inhabiting pests such as imported fire ants impact management-oriented, soil quality and crop nutrient assessment efforts at field-, landscape-, and perhaps regional scales; however, the temporal stability of ant-mediated changes in the soil matrix is poorly understood.

Some of the results from this study as well as much of the work conducted by predecessors (who focused on pH, N, P, K⁺, and bulk density) serve to underscore the transient nature of imported fire ant mound physicochemical properties as well as aspects of site-specific variability (attributed to soil heterogeneity) encountered in response to imported fire ant mound construction. In this investigation carried out on silt loam soils, mound pH was consistently higher than undisturbed soil during two key phases in the ants' annual cycle. Nitrogen levels, on the other hand, were significantly different in ant mound versus control soil environments in September only (at or near peak biomass in an agroecosystem irrigated on a near-weekly basis), whereas total N content between these two soil environments was not significantly different in December. Lafleur et al. (2005) reported that NH₄⁺-N from S. invicta mound soil was sharply elevated compared to undisturbed soil from long-leaf pine forests and plantations in Louisiana (though they did not verify that higher mineral N availability was not simply due to higher total N pools in ant mound soils). Turfgrass harvested from ant mound perimeters in September was

substantially higher in total N than turfgrass in control plots; undoubtedly in response to the available surplus.

Nitrogen (N) content in select plant species (e.g., corn) has been correlated with reflectance in the green and near-infrared (NIR) spectral bands (e.g., Bausch and Duke, 1996) as a result of differences in chlorophyll content, therefore it is reasonable to propose that higher N levels expressed in the grasses surrounding imported fire ant mounds may be a useful indicator (at certain times of the year) in improving the detectability of remotelysensed ant mound features. Chen (2007) recovered uric acid, urea, and amino acids from artificial nest particles stained with ant excretions. He hypothesized that Ncontaining excretory compounds and phosphoric acid may contribute to the abundant vegetation commonly found around fire ant mounds; earlier investigators (Herzog et al., 1976; Green et al., 1977, 1998, 1999) had suggested excreta as a source of element enrichment in S. invicta mound soils. However, results from this study document the concurrent associations of nutrient availability in imported fire ant mound soils with enhanced nutrient levels expressed in perimeter vegetation (i.e., N, P, Ca²⁺, S, Cu²⁺, Fe²⁺, and Na⁺), which, in turn, may help refine remote-sensing detection tools useful in identifying and monitoring imported fire ant infestations in agronomic and urban settings.

Phosphorus (P) tends to be strongly adsorbed (or fixed) to soils, especially clay-rich soils (e.g., Tisdale et al., 1993); however, active turfgrass growth may interact (or "interfere") with P accumulation in the ant mound environment because this element is an essential plant macronutrient. Turfgrass collected from ant mound perimeters in September was significantly higher in P content compared to undisturbed (control) vegetation. Phosphorus (P) accumulation in imported fire ant mounds may resume when the vegetation goes dormant, as suggested by evidence from the current study. In turn, P accumulation (as phosphoric acid from ant excreta and other aforementioned sources) may be linked, in part, with the overall decline in ant mound soil pH recorded in December.

Potassium availability (K^+) is influenced by a variety of soil factors including soil texture, types of clay minerals present, and the capacity of the soil to fix K^+ . Plant factors (e.g., root type and density) also affect K^+ availability (Tisdale et al., 1993). Significant contrasts in K^+ availability in ant mound soils versus control soils were only evident for the late Autumn to Winter transition (December) during turfgrass dormancy; at this time, K^+ retention in ant mound soils was substantially higher.

Comparative examination of other macro- and micronutrient "gains and losses" in ant mound versus control soil environments from September to December highlight additional emergent patterns of retention or translocation. For example, continued pedoturbation by imported fire ants combined with resident metabolites resulted in Ca²⁺ retention in mound soils versus substantial loss of this macronutrient from undisturbed soils in December. A reasonable explanation for the enhanced stability of Ca^{2+} in mound soils is related to the fact that this divalent cation oftentimes replaces micronutrients from chelates in agronomic settings, because the concentration of Ca^{2+} in the soil solution is much greater than the concentrations of available micronutrients (Brady and Weil, 2002). During the late Autumn to Winter transition, the mean Ca^{2+} concentration of ant mound soil is close to 1.7 times greater than the control soil.

Chelating compounds (typically in the form of low-molecular weight organic acids) are continually produced by microbes, plant roots (which release organic anion exudates; the latter topic has been reviewed by Ryan et al., 2001), and from the decomposition of soil OM (e.g., McColl and Pohlman, 1986). Recently, over twenty organic acids have been reported from *S. invicta* excreta recovered from artificial nests constructed in silica gel (Chen, 2007). Chen (2007) commented on the antimicrobial function of lactic, benzoic, and malic acids all of which are widely-used food preservatives for human consumption, and suggested that the presence of these organic acids in *S. invicta* ant nests may have a substantial impact on the resident microbial community, which may, in turn, affect colony fitness.

Low-molecular weight organic acids are known to have short retention times in soils (e.g., Stevenson, 1967; Jones et al., 1996), however, they are continually replenished by soil biota metabolic and decomposition processes. These substances are important in the cycling of trace elements as well as to soil acidity (Stevenson, 1986; Sposito, 1989) and offer a partial explanation for some of the contrasts in the temporal partitioning of soil chemical changes from ant mound versus control soil environments reported in this study. Exudation of organic anions by plants such as malate and malonate (the proton-dissociated forms of malic acid and malonic acid) are known to complex to varying degrees with Al³⁺, Fe³⁺, Ca²⁺, Cu²⁺, Mn²⁺, and Zn²⁺ (Bar-Yosef, 1991; Bolan et al., 1994). So, it is highly probable that select organic acids produced by imported fire ants (i.e., malic, malonic, and possibly others) and deposited in nest soil may serve dual roles, functioning as both antimicrobial and chelating agents, or alternatively, some of these chemicals may contribute to the antimicrobial arsenal, whereas others may serve to either enhance nutrient availability to the ants or function as cheluviation agents by naturally eliminating potential toxicants (e.g., Fe²⁺, Mn²⁺ – Table 1) from mound environments. These imported fire ant metabolites represent an amplification of the host of low molecular-weight organic acids already available in these disturbed soils (i.e., root exudates, microbial metabolites, and products of OM decomposition); thus, providing additional evidence that imported fire ant mound environments are transient "hot spots" for macronutrient/micronutrient accumulation (e.g., Ca²⁺, Zn^{2+} – Table 1) as well as mobilization.

Response of control soils differed from ant mound soils in P, K^+ and Zn^{2+} concentrations from one seasonal transition to the next, including: (1) substantive losses of

 K^+ (P=0.0049) presumably due to leaching; (2) rather sharp declines in P (P=0.0573); contrasting with (3) rather notable increases in Zn^{2+} (P=0.0647). Significant increases in Cu^{2+} and S occurred in both imported fire ant mounds and control soils, whereas Mn^{2+} concentration declined substantially from both soil environments over this 12+ week interval. The careful detailing of imported fire ant assimilation/dissimilation effects on soil chemistry as well as their influences on soil processes (e.g., nutrient cycling) in select agroecosystems, and, perhaps most importantly at key stages in their annual cycle, may reveal avenues for the development of well-integrated biological-geochemical control techniques or better management practices for curbing their spread into disturbed environments.

The longer-term impacts of mound age and site fidelity were impossible to ascertain in this sod production agroecosystem. This observation is in agreement with researchers investigating other aspects of imported fire ant population ecology dynamics (e.g., Tschinkel, 1988; Cook, 2002). Frequent mowing in sod production environments pre-empted the investigation of nutrient stratification (as conducted by Lockaby and Adams, 1985), for imported fire ant mounds were repeatedly truncated 2–3 times per week during the growing season by mowers. In addition, turfgrass harvesting in some tract corridors resulted in imported fire ant mound locations shifting from week to week in response to turf removal (DeFauw, 2006, pers. obs.).

Sod production environments appear to represent the most unstable of the agroecosystems that invasive Solenopsis spp. regularly colonize and successfully reinfest. Yet, the biogeochemical signatures that develop in these imported fire ant mounds (presumably over the course of a few to several months) are discernable and a partial history of the temporal patterning of nutrient availability in the ant mounds at two key phases in their annual cycle has emerged from a turfgrass production agroecosystem dominated by silt loam soils. The interactions of ant-mediated soil modifications with the chemical contributions from plants and other organisms co-existing in the mound environment, as well as a host of abiotic factors linked to mineral soils may significantly influence colony fitness. Tracking seasonal changes in the biogeochemistry of imported fire ant mound soils may have important implications in elucidating the sitespecific success of epizootiological events for some of the agents of classical biological control (e.g., the microsporidium Thelohania solenopsae Knell, Allen, and Hazard). Therefore, continued detailed documentation of invasive Solenopsis spp. mound soil ecosystem dynamics (involving multiple agronomic systems as well as landscape settings) in tandem with improved knowledge of the site-specific requirements of known imported fire ant pathogens and parasites is warranted.

Acknowledgements

M. Guadalupe Rojas (USDA, ARS, National Biological Control Laboratory, Biological Control of Pests Research Unit), Douglas A. Streett (USDA, ARS, NBCL, BCPRU), F. Aubrey Harris (Mississippi State University, Delta Research and Extension Center) and two anonymous reviewers provided thoughtful comments on an earlier draft of this manuscript. Jian Chen and Margaret L. Allen (USDA, ARS, NBCL, BCPRU) are kindly thanked for GC-MS and PCR analysis, respectively. Al Martin (USDA, ARS, NBCL, BCPRU) is thanked for his capable assistance in the field.

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